the successive backcrosses have increasing dosages of the K genotype, a more rapid breakdown might have been expected.

The second series of backcrosses was carried out to collect additional data. to test for the occurrence of breakdown, and to obtain breakdown individuals for a compatibility test with S stock. There was a complete absence of breakdown up to and including the $B_{6k}\beta$ generation (Table 2). A third series of backcrosses was made solely to check the occurrence of breakdown, and the result was also negative. It seems probable that the breakdowns in the first experiment may have been due to an accidental contamination of the $F_1 \times K$ mating with a K female. The complete inviability of eggs

TABLE 3.
Repeat Experiment to Test for "Breakdown".
(Each mating of approx. 130 and 150.)

Serial No.	Cross.	Progeny Designation.	No. of Eggs.	Hatch.	Percentage Hatch.
1	$F_1^{\alpha} \times K^{\beta}$	B_{1k}^{α}	normal	normal	high
2	$K^{\beta} \times F_1^{\alpha}$	B_{1k}^{β}	5600	0	0·0
3	$B_{1k}^{\alpha} \times K^{\beta}$	B_{2k}^{α}	normal	normal	high
4	$K^{\beta} \times B_{1k}^{\alpha}$	B_{2k}^{β}	6894	0	0·0
5	$B_{2k}^{\alpha} \times K^{\beta}$	B_{3k}^{α}	normal	normal	high
6	$K^{\beta} \times B_{2k}^{\alpha}$	B_{3k}^{β}	6962	0	0·0
7	$B_{3k}^{\alpha} \times K^{\beta}$	B_{4k}^{α}	normal	normal	high
8	$K^{\beta} \times B_{3k}^{\alpha}$	B_{4k}^{β}	5368	0	0·0
9	$B_{4k}^{\alpha} \times K^{\beta}$	$B_{5k}\alpha$	normal	normal	high
10	$K^{\beta} \times B_{4k}^{\alpha}$	B_{5k}^{β}	5054	0	0·0

derived from K females and S maternal line males is maintained up to the $B_{6k}\alpha$ generation, and probably indefinitely. $B_{5k}\alpha$ individuals, predominantly K in genotype, however, show full fertility and high egg viability when crossed to S stock in either direction. The strictly maternal inheritance of some determinant, either on a chromosome or in the cytoplasm, is demanded.

Sex ratio. Data on sex ratios in S and K stocks, and in F_1 hybrids are presented in Tables 4 and 5. In all cases there is a significant surplus of males, approximating to a ratio of 1·25:1. The most probable cause of this inequality is differential mortality. Males mature and emerge several days earlier than females, and the last larvae to pupate in any culture are invariably female. In the larval and pupal cultures, the death rate increases gradually with time, and there is no reason to assume other than a normal genetic sex determination.

Segregation in the F_2. The two subspecies differ in a small but distinctive character. In K there is a line of white scales on the anterior surface of the femur of the mid-leg, and this line is absent in the S race. In the F_1 there is a thin broken line, indicating an absence of dominance. In the F_2 there is segregation for the character indicating a monofactorial mendelian inheritance independent of sex (Table 6). Actually the genetic control of the character is complex, and probably modifier genes influence its degree of

development. The significance of the segregation for the present purpose lies in the independence of a major "line" gene and the sex chromosome. Normal meiotic segregation is indicated for two of the three chromosome pairs present in *Aëdes*.

The inbreeding program. In the *Aëdes scutellaris* group, mating seems to be conditional on the formation of swarm flights of males, and multiple copulations may occur for each female entering the swarm. Such a system seems adapted to the maintenance of genetic heterogeneity.

TABLE 4.

Sex Ratios.

Culture.	Females.	Males.	Total.	Sex Ratio.
S. 52/5B	176	330	516	1 : 1·87
52/11–B	92	214	306	1 : 2·36
52/7–B	215	201	416	1 : 0·94
Total S	483	745	1238	1 : 1·54
K. 52/1–B	39	45	84	1 : 1·15
52/4–B	239	312	551	1 : 1·31
52/10–B	105	84	189	1 : 0·80
Total K	383	441	824	1 : 1·15
S × K (F_1)*	546	672	1218	1 : 1·23

* See analysis in Table 5.

A need was felt for the isolation of genes with a marked phenotypic effect for use as markers of chromosome segregation. An inbreeding program was commenced with the laboratory stock S, and based on the plan outlined by Spencer (1947). Mass matings were made, and were given two blood feedings within three days. Gravid females were then immediately isolated in 8″ × 1″ tubes, each with a pad of wet filter paper, and the

TABLE 5.

Sex Ratio in S × K Progeny.

Egg Batch.	Date Laid.	Date Sown.	Number of Eggs.	Hatch.		Adults Reared.			% Survival.	Sex Ratio.
				No.	%	♀	♂	Total.		
1	25–26/2/52	3/3/52	39	19	48·7	5	11	16	84·2	1 : 2·22
2	26–27/2/52	,,	139	96	69·1	24	31	55	57·3	1 : 1·39
3	27–29/2/52	,,	167	152	91·0	69	74	143	94·1	1 : 1·07
4	29/2–3/3/52	,,	506	501	99·0	177	217	393	78·4	1 : 1·22
5	3–4/3/52	10/3/52	86	7	8·1	2	2	4	57·1	1 : 1·00
6	4–7/3/52	,,	465	308	66·2	105	132	237	74·5	1 : 1·35
7	7–10/3/52	,,	655	315	48·1	113	108	221	70·1	1 : 0·95
8	10–17/3/52	17/3/52	425	201	47·3	60	105	165	79·0	1 : 1·70
Total			2482	1499	60·4	546	672	1218	81·2	1 : 1·23

tubes were sealed with cotton plugs. Egg laying commenced and continued for 5 to 14 days without further blood feeding. From each family of progenies, sib mass matings were made, and females isolated as before. On the assumption that females copulate repeatedly, each female initially isolated would carry a sample of the sperm produced by the available males. Should any initially isolated female be heterozygous for an uncommon recessive gene *a*, 50% of its progeny would be *Aa*. In the subsequent sib mass mating, 25% of the sperm would be *a*. If three females are isolated from the sib mating there would be an 82½% chance that at least one would be *Aa*, and its progeny should show 12½% of homozygous recessives.

The results of this program are given in Tables 7A and 7B. No success was achieved in the isolation of recessive genes. Possibly the laboratory stock had lost genetic heterogeneity over four years and perhaps 25 generations of artificial culture. Probably the mutant characters likely to be most frequent would be inconspicuous to casual inspection. Nevertheless the results are of considerable interest.

TABLE 6.

F_2 Segregation for White Scales on Midfemur.

	"White."	"Intermed."	"Black."	Total.
Females ..	52	90	51	193
Males ..	33	91	48	172
Total ..	85	181	99	365

Total data: Fit to 1 : 2 : 1 ratio. $\chi^2 = 1{\cdot}08$. 2d.f. $P = 0{\cdot}6$.
Independence of sex linkage: $\chi^2 = 5{\cdot}21$. 5d.f. $P > 0{\cdot}3$.

Reference to Table 2 shows that, under the artificial breeding conditions of the laboratory, there is a considerable difference in fecundity between S and K females. There is no significant difference between self and cross matings, and the lower fecundity of the K females appears to be dominant in the F_1.

TABLE 7A.

Egg Laying of Isolated Females.

Individual Female.	Eggs Laid.	Hatch.	Hatch Percentage.	Means for Inbred Daughters.	
				Eggs Laid.	Percentage Hatch.
52/11·1	24	20	83·3	38·5	31·6
52/11·2	58	34	58·6	24·7	37·4
52/11·3	50	36	72·6	27·2	59·5
52/11·4	29	19	65·5	17·3	33·3
52/11·5	85	59	69·4	29·7	39·3
52/11·6	96	50	52·1	32·0	8·7
52/11·7	56	34	60·7	46·2	33·0
52/11·8	50	30	60·0	26·8	66·7
52/11·9	30	19	63·3	1·0	0·0
52/11·10	35	30	85·7	19·0	67·5
52/11·11	29	24	82·7	56·6	54·1
52/11·13	32	26	81·2	38·5	51·9
52/11·14	80	60	75·0	13·3	22·6
52/11·15	42	37	88·1	18·5	55·7
52/11·16	11	0	0·0	—	—
52/11·17	19	17	89·5	—	—
52/11·18	31	0	0·0	—	—
52/11·19	14	14	100·0	26·0	23·1
52/11·20	53	43	81·1	29·6	40·6
52/11·21	48	42	87·5	39·0	52·1
52/11·22	19	0	0·0	—	—
52/11·23	139	131	94·2	16·3	39·1
Total	1030	725	70·4	—	41·7
Mean	46·8	—	—	24·7	—

TABLE 7B.

Egg Laying of Inbred Females.

Individual.	Eggs Laid.	Hatch.	Hatch %
52/11· 1– 1	42	20	
2	32	3	
3	35	20	
4	49	7	
M.	*39·5*	—	*31·6*
52/11· 2– 1	11	7	
2	25	20	
3	4	0	
4	59	10	
M.	*24·7*	—	*37·4*
52/11– 3– 1	45	30	
2	39	27	
3	7	0	
4	3	2	
5	61	37	
6	8	1	
M.	*27·2*	—	*59·5*
52/11· 4– 1	23	8	
2	0	0	
3	17	4	
4	29	11	
M.	*17·3*	—	*33·3*
52/11· 5– 1	51	21	
2	22	8	
3	16	6	
M.	*29·7*	—	*39·3*
52/11· 6– 1	59	0	
2	1	0	
3	2	0	
4	1	0	
5	97	14	
M.	*32·0*	—	*8·7*
52/11· 7– 1	40	0	
2	44	0	
3	43	38	
4	33	26	
5	53	0	
6	34	7	
7	76	39	
8	47	12	
M.	*46·3*	—	*54·1*
52/11· 8– 1	58	48	
2	0	—	
3	0	—	
4	38	Lost	
5	38	16	
M.	*6 8*	—	*66·7*
52/11· 9– 1	3	—	
2	1	0	
3	3	0	
4	0	—	
M.	*1·0*	—	*0·0*
52/11·10– 1	46	37	
2	1	0	
3	0	—	
4	49	40	
5	0	—	
6	18	0	
M.	*19·0*	—	*67·5*
52/11·11– 1	62	35	
2	53	44	
3	53	12	
M.	*56·0*	—	*54·1*
52/11·13– 1	70	37	
2	7	3	
M.	*38·5*	—	*51·9*
52/11·14– 1	0	—	
2	6	1	
3	26	17	
4	38	0	
5	22	3	
6	0	—	
7	1	0	
M.	*13·3*	—	*22·6*
52/11·15– 1	17	17	
2	41	0	
3	1	0	
4	0	—	
5	0	—	
6	21	21	
7	0	—	
8	1	0	
9	1	0	
10	41	31	
11	71	39	
M.	*18·5*	—	*55·7*
52/11·19– 1	0	—	
2	52	12	
M.	*26·0*	—	*23·1*
52/11·20– 1	0	—	
2	39	29	
3	89	25	
4	10	2	
5	0	—	
M.	*29·6*	—	*40·6*
52/11·21– 1	59	35	
2	58	26	
3	0	—	
M.	*39·0*	—	*52·1*
52/11·23– 1	0	—	
2	29	6	
3	0	—	
4	28	19	
5	49	24	
6	49	5	
7	43	16	
8	3	0	
9	10	5	
10	9	4	
11	16	12	
12	18	9	
13	2	0	
14	0	—	
15	0	—	
16	5	2	
M.	*16·3*	—	*39·1*
Total ..	2422	1010	41·7
General mean	24·7	—	—

Isolated females of race S show considerable variation in fecundity, but the mean, 46·8 eggs per female, is comparable with the figure obtained for S females in mass culture (Table 7A). The mean hatching, as a percentage of total eggs, was 70·4% in the isolations, and 71·1% in the mass culture. Among the inbred daughters, many failed to oviposit, and the means, eggs per female (24·7) and hatching (41·7%), were much lower. The figures suggest a marked degree of inbreeding depression.

The time of action of lethality. In a considerable proportion of eggs derived from K × S and B × S matings, sperm heads have been seen in the egg cytoplasm if the eggs are crushed in aceto-orcein within half an hour of oviposition. Similar observation of 6-hour eggs indicates that some at least undergo early embryonic development. Inviability is not due to any failure of sperm to penetrate the eggs, but rather to an incompatibility between the sperm, or the hybrid embryo, and the egg cytoplasm.

In viable eggs of *Aëdes scutellaris*, and in S × K hybrids, development is very rapid, and an almost fully developed embryo is produced in 48 hours. In the inviable K × S eggs, death ensues at an early stage, and after 24 hours they show a definite collapse. Lethality is effective either before or during the cleavage divisions, or in the early blastoderm—i.e., in the stage 1 of Hadorn's (1948) classification of *Drosophila* lethals. In contrast, lethality in Laven's *Culex molestus* hybrids (Laven, 1953) is effective much later, during late embryonic stages, or during or shortly after hatching. The *Culex molestus* lethality is also characterized by a much lower penetrance.

Discussion.

It is neither desirable nor possible to attempt an adequate discussion of the data presented in the present paper without a consideration of the main features of non-reciprocal fertility in other groups of the Culicidae. In particular, the results obtained by Laven (*l.c.*) in *Culex* and by us in *Aëdes* show such a close parallelism that they must be dependent on similar genetic mechanisms.

1. *Possible genetic mechanisms.*

At the present stage, several possible genetic mechanisms must be considered, if only for the summary rejection of some. Parthenogenesis and pseudogamy can be dismissed on the basis of the F_2 segregations given in Table 6. Laven (1953) and Toumanoff (1950) also give evidence eliminating parthenogenesis, but Downs and Baker (1949), Bonnet (1950), and Perry (1950) find some support for its assumption.

Hypotheses of predetermination, of the *Limnaea* type, are incompetent to explain the behaviour. A possible system of multiple incompatibility (*s*) genes affecting the survival of S or of hybrid sperm in K egg cytoplasm, suggested by Smith-White (1950), is denied by Laven's and our own results. Such a system should give a uniformly increasing rate of breakdown in the later backcross generations, the actual rate depending on the number of *s* genes involved, and on their linkage relationships. In our material, breakdown is absent or extremely rare, and in Laven's there was a constant rate of breakdown up to the 11th backcross generation. Both cases are characterized by their permanence, and neither is affected by the building up of K or O* genoms, respectively, in the backcrosses.

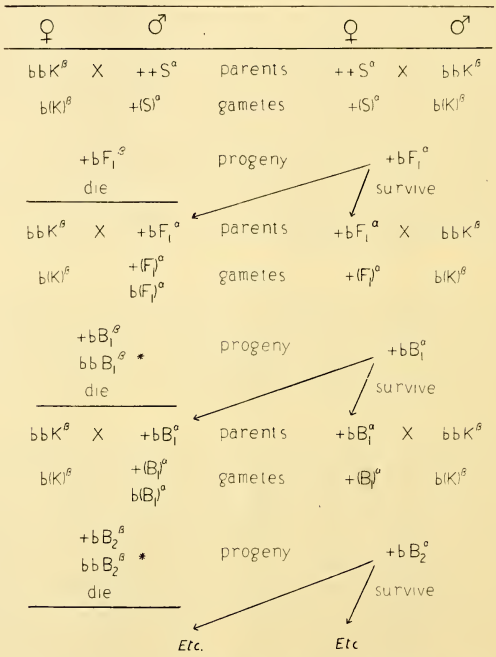
In a female-heterozygous sex system, a sex-linked incompatibility-lethal could explain both the *Culex* and *Aëdes* systems, with breakdown due to crossing over between the lethal and sex genes. However, Gilchrist and Haldane (1947) have demonstrated a male-heterozygous sex-system in *Culex molestus*, and this type of sex determination is characteristic of the Nematocera (White, 1949).

Two kinds of genetic mechanisms remain. One is chromosomal, and is dependent on the uniparental inheritance of chromosomes or of chromosome segments, and involves anomalies of the meiotic cycle. The other is nucleus-independent and cytoplasmic.

Very peculiar meiotic cycles are known to exist in other families of the Nematocera. In *Sciara* the chromosomes of paternal origin are eliminated during spermatogenesis

* O is the symbol used by Laven for his Oggelshausen strain of *Culex molestus*.

(Metz, 1938). In *Miastor* and other genera of the Cecidomyidae, many chromosomes are eliminated in spermatogenesis, and are transmitted only in the female line. In the Culicidae, limited chromosomes are not present. In *Culex* (Callan and Montalenti, 1947) and in *Aëdes* chiasmata are formed in all three bivalents in male meiosis. Moreover, in *Aëdes scutellaris*, the approximately normal sex ratio, and the sex independent segregation of "line" provide genetic evidence for the normal meiotic separation of two of the three chromosome bivalents.



Text-figure 2.—Gene control of non-reciprocal fertility, dependent on the elimination of a paternal chromosome segment in oogenesis.

The symbols K, S, F_1, B_1, etc., refer to the *unlimited* gametic genoms. *b* and + are alleles which condition the cytoplasm, and are carried on limited (maternally-inherited) chromosome segments.

Note.—Sperm $b(F_1)^{\alpha}$ from *a* males are unadapted and hybrids derived from unadapted sperm and $b(K)^{\beta}$ eggs die.

It is possible to devise chromosomal systems of permanent non-reciprocal fertility on the basis of two assumptions. There must be a strictly polarized segregation of a chromosome segment in oogenesis, with the elimination of the segment of paternal origin in hybrids. It is not necessary to assume any similar elimination in spermatogenesis, and the sperm wastage which would result from such behaviour is not evidenced. In oogenesis, the paternal segment must be directed into the polar bodies. The second necessary assumption is the existence of a cytoplasm-conditioning gene, carried on the polarized chromatin, in one or other of the two species or races involved. An example of this type of hypothesis is offered in Text-figure 2. Race K is there considered to be homozygous for the cytoplasm-conditioning gene "bar" or "*b*", carried on polarized

chromatin, which modifies the cytoplasm from a neutral α condition to a β condition, intolerant of other than *b*-adapted sperm or hybrid embryos. Race S is inferred to be homozygous for a neutral or + allele at the same locus. In this scheme, + must be dominant to *b*, and there must be a lag of several cell generations in cytoplasmic adaptation following a change of genotype. Consequently *b* sperm from *b*+ males are initially unadapted.

The assumption of lag in the conditioning of the cytoplasm is necessary to allow partial embryonic development. Exceptional breakdown is permitted by a slight variability in the penetrance of the lethal effect following the fertilization of $b(K)\beta$ eggs by $b(F_1)\alpha$ or similar unadapted sperm, thus allowing cytoplasmic adaptation in the $bb(B_1)$ embryos.

There is no cytological or genetical evidence to support the inference of meiotic polarization which hypotheses of this type require, but if this inference is rejected, an explanation based on cytoplasmic inheritance independent of the genotype must be invoked.

Cytoplasmic inheritance is known in many plants (cf. Caspari, 1948) and in some animals. Laven (1953) has already drawn attention to the similarities between the known cases of plasmagenic or genoid inheritance in *Paramoecium* and in *Drosophila* and the inheritance of non-reciprocal fertility in mosquitoes, and it is unnecessary to elaborate this comparison further. A plasmagenic hypothesis can be set up in simpler form than the chromosomal scheme given in Text-figure 2, but is in fact very similar in operation. It is only necessary to regard the cytoplasmic conditions α and β as being independent and self-perpetuating. Breakdown could occur either by a variable penetrance of the lethal effect of the β plasmagene, or by the possibility that sperm could occasionally carry a sufficient dosage of β to enable them to survive in β egg cytoplasm.

At present there is no evidence enabling a choice to be made between hypotheses of uniparental inheritance of cytoplasm-conditioning genes and cytoplasmic inheritance.

2. *The role of non-reciprocal fertility in speciation.*

On present knowledge, the S and K races of *Aëdes scutellaris* are geographically isolated, and they are morphologically distinguishable. It is probable that the genetic basis of their non-reciprocal fertility was able to develop because of their geographic isolation. In Laven's races of *Culex molestus* a geographical factor is also apparent.

In crosses between *Aëdes aegypti* and *A. albopictus*, various authors have obtained conflicting results. Downs and Baker (1949) and Bonnet (1950) found that fertile hybrids could be obtained only by using *A. aegypti* females. The reciprocal mating gave effective insemination and egg laying, but the eggs were inviable. Both authors suggested parthenogenesis as a possible explanation. Toumanoff (1939, 1950) obtained exactly the opposite results, a fertile F_1 being obtained only when *A. albopictus* was the maternal parent. Toumanoff's strains of the two species were obtained independently of those of Downs and Baker and Bonnet. Simmons, Saint John and Reynolds (1930) were unable to cross the same two species in either direction, and were unable to obtain egg laying in their matings. DeBuck (1942) obtained normal egg production in matings between the two species in both directions, but the reciprocal F_1s were both inviable. He found that with *A. albopictus* as maternal parent hybrid eggs showed no embryonic development, but in the reciprocal cross some embryonic development was usual. His results indicate a reciprocal difference in the same direction as those of Downs and Baker and Bonnet, but with a higher degree of incompatibility.

A. aegypti and *A. albopictus* must include geographical races differing in mating type. It is suggested that the degree of isolation indicated in DeBuck's results is causally related to the partial isolation reported by Downs and Baker, and to the absolute isolation found by Simmons *et al.* Partial, non-reciprocal isolation may represent a stage in the origin of complete isolation, and may constitute a significant factor in speciation.

In crosses between *Aëdes hebrideus* and *A. pernotatus* Perry (1950) found that viable eggs were only obtained when *A. hebrideus* was the maternal parent, but that only a small proportion of the females of that species (3 out of 37) yielded viable progeny. Hovanitz (1946) found considerable variation in the fertility of individual females of *Haemogogus* sp. when mated to their own males, and we find a similar variability in isolated females of *A. scutellaris*. It is possible that a species-population may be heterogeneous for sterility factors. Fixation of mating type in geographical isolates would then be expected, and the conflict between the results of the various authors could be understood.

In the *Culex pipiens* species complex an apparently confused picture of relationships comes from an analysis of the available interfertility data. Marshall (1938) found that races of *C. molestus* from Paris and London which were reciprocally intersterile, both

Text-figure 3.—Race relationships in the *Culex pipiens* complex.

Key:

⟷ Full reciprocal compatibility.
⟷ Partial reciprocal compatibility.
♂ ♀
⟶ Non-reciprocal compatibility.
– – – – Complete incompatibility.

F, Farid, 1949; L, Laven, 1951, 1953; M, Marshall, 1938; R, Roubaud, 1941; TV, Tate and Vincent, 1936; W, Weyer, 1936.

gave viable eggs and fertile F_1 progeny when mated to males of a strain from Hayling Island, and inviable eggs in the reciprocal crosses. Laven (*l.c.*) found that various isolations of the same species could be grouped on a geographical basis. Isolations from north-eastern Germany and western Europe were intersterile in both directions, and both were fertile with isolations from southern Germany only when the latter strains were used as male parents. It is noteworthy that Laven's isolations from London and Paris were fully interfertile, whereas Marshall's strains from the same localities were reciprocally intersterile.

Tate and Vincent (1936) were able to cross *C. molestus* and *C. pipiens* in both directions. Weyer (1936) found full fertility between *C. molestus* and *C. fatigans* but was unable to cross *C. pipiens* and *C. fatigans*. Farid (1949), however, found the last two species to be fully and reciprocally interfertile, and Roubaud (1941) working with

the same species obtained results suggestive of a reciprocal difference (*fatigans* × *pipiens*, 300 eggs, 55 larvae; *pipiens* × *fatigans*, 850 eggs, 2 larvae).

It is again apparent that races in the *C. pipiens* complex differ in factors affecting interracial fertility, and that these differences have a geographical basis. However, interracial fertility barriers are not conformable with the recognized species limits in the group, and it would seem unlikely that they represent stages in speciation parallel with those involved in the origin of *C. pipiens*, *C. molestus* and *C. fatigans*. We are inclined to agree with Mattingly (1951) that the whole group should be recognized as a single species, with many geographical subspecies and locality races.

The role of non-reciprocal fertility in the origin of total isolation and speciation is problematical, but it is of particular interest as a possible evolutionary mechanism. Perhaps intrinsic isolation and speciation may arise, on occasion, firstly in the cytoplasm, and secondarily in the nuclear genom.

Summary.

A study has been made of the inheritance of non-reciprocal fertility in two subspecies of *Aëdes scutellaris*, *A. s. scutellaris* and *A. s. katherinensis*.

Mating type shows a strict maternal inheritance. F_1 eggs from subsp. *scutellaris* (S) females and subsp. *katherinensis* (K) males are normally viable, and are of S mating type. Backcrosses of F_1 females to K males are viable, and again, are of S mating type. In successive backcrosses to K males, to the B_6 generation, the S mating type is retained. All crosses involving K females yield inviable eggs, and it is not possible to test the mode of inheritance of the K mating type.

The results obtained are essentially similar to those reported by Laven for mating type inheritance in *Culex*, but the lethal effect in inviable eggs is earlier in operation, and more severe, in *Aëdes* than in *Culex*.

Meiosis in the male is apparently normal. The genetic system determining the inheritance of mating type must depend either on anomalous meiosis in oogenesis, with a polarized segregation of bivalents and the elimination of part of the paternal genom, or on nucleus-independent cytoplasmic factors. There is no critical evidence enabling a choice between the two types of hypothesis. The observed entry of sperm into eggs in the inviable matings, partial embryonic development in the inviable *Culex* matings, and F_2 segregation in viable S female × K male matings, allow the rejection of hypotheses of parthenogenesis.

From a consideration of the available data on mating isolation between species and races of *Aëdes* and *Culex*, the type of non-reciprocal fertility described is considered to be significant as a source of incipient speciation in mosquitoes.

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A NEW *COPTOTERMES* AND *AHAMITERMES* (ISOPTERA) FROM AUSTRALIA.

By F. J. Gay.*

(*Communicated by Dr. A. J. Nicholson.*)

(One Text-figure.)

[Read 29th September, 1954.]

Synopsis.

A new mound-building species of *Coptotermes* with which is associated a new species of *Ahamitermes* has been collected in Western Australia. Descriptions of these two species are given together with brief notes on their biology.

Introduction.

During the past two years officers of the Wildlife Survey Section of the Commonwealth Scientific and Industrial Research Organization have carried out a number of extensive survey trips in Western Australia. As a spare-time activity, one of the officers, Mr. J. H. Calaby, has given special attention to the termite fauna and, as a result, has collected some hundreds of series that have yielded considerable information on the range of distribution of most of the species recorded from this State by Hill (1942), established the presence of several species not previously known to occur in Western Australia, and have included some hitherto undescribed species.

The termites described below were collected during a recent survey trip north of Geraldton, and I am indebted to Mr. Calaby both for this interesting material and for the excellent and detailed field notes that accompanied the collection.

It may seem a little strange that such a conspicuous and distinctive species as the new *Coptotermes* described below should not have been recorded previously, but this may be due to its restriction to a relatively small area in a sparsely settled and infrequently travelled region.

The association of a new species of *Ahamitermes* with the new species of *Coptotermes* is not altogether unexpected, since this association between the two genera occurs commonly on both sides of the continent. Indeed the specificity of this association is such that it would have been a little surprising if the *Ahamitermes* found in the mounds of such a distinctive species of *Coptotermes* had not been new.

The drawings of the soldier and alate heads were made with the aid of a camera lucida.

Coptotermes brunneus, sp. nov.

Winged Adult (Fig. 1, A).

Medium sized, head, thorax, and tergites of abdomen very dark brown (almost black), sternites of abdomen somewhat paler. Legs of varying shades of brown, the distal portions of the tibiae and the tarsi yellowish. Basal segment of the antenna the same colour as the head, the remaining segments, palps, postclypeus and labrum, golden brown variably suffused with darker brown. Wing stumps dark brown, the basal portion of the media and cubitus and the wing membrane between the radial sector and costal border brown, the remainder of the wing membrane pale fuscous. Head, thorax, wing stumps, and abdomen hairy. Head narrowed in front of the eyes, hemispherical behind. Antennae of 20 segments, third segment generally shortest and narrowest of all; occasionally fourth segment shortest of all. Postclypeus more than three times as wide as long. Eyes moderately large; ocelli 0·10 to 0·14 mm. long and separated by about half their length from the eyes. Fontanelle small and indistinct.

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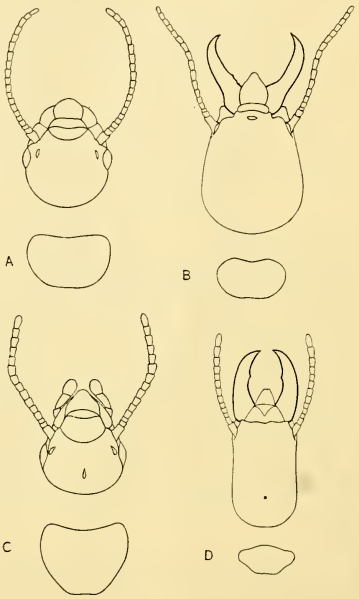
Pronotum somewhat narrower than head and conspicuously wider than long, anterior margin widely and shallowly concave, sides but little rounded, the postero-lateral corners almost straight and the posterior margin slightly sinuate. Anterior wing stump very large, almost twice as long as that of hindwing. Costal border, radial sector and basal sections of media and cubitus well defined, the remainder of the veins weakly developed. Wing membrane without hairs, densely covered with micrasters.



Text-figure 1.

A, *Coptotermes brunneus*, n. sp. Head and pronotum of winged adult. B, *C. brunneus*, n. sp. Head and pronotum of soldier. C, *Ahamitermes inclusus*, n. sp. Head and pronotum of queen. D, *A. inclusus*, n. sp. Head and pronotum of soldier.
(Camera lucida drawings by Miss B. J. Gemmell.) (A, B, × 10; C, D, × 16.)

Measurements (50 specimens).—Length, with wings, 10·50–13·00 mm.; length, without wings, 6·20–8·00 mm.; head, to apex of labrum, long, 1·59–1·81 mm.; head, to clypeofrontal suture, long, 1·08–1·21 mm.; head, wide, 1·41–1·54 mm.; eyes, maximum diameter, 0·34–0·40 mm.; ocelli, long, 0·10–0·14 mm.; pronotum, long, 0·77–0·84 mm.; pronotum, wide, 1·28–1·41 mm.; forewing, long, 8·20–8·90 mm.; forewing, wide, 2·20–2·50 mm.

Soldier (Fig. 1, B).

Large, somewhat variable in size, with a very large head. Head and pronotum raw umber, meso- and metanotum progressively paler; abdominal tergites about the same colour or a little paler than the metanotum, a pale median line extending from the front of the pronotum to the second or third abdominal tergite. Femora somewhat fuscous, tibiae pale brown. Head darkest anteriorly, basal segment of antenna the same colour as the anterior portion of the head, second segment pale golden yellow, the remaining segments as well as those of the maxillary palps variably suffused with brown. Labrum bright golden yellow, the central area suffused with brown, with a

hyaline tip. Mandibles dark ferruginous. Head and thorax with a moderate number of stout reddish hairs, abdomen very hairy. Head longer than wide, very little rounded on the sides, narrowing evenly to the anterior margin, generally widest at the posterior third and broadly rounded behind. Antennae of 17–18 segments, third segment generally shortest of all, occasionally third and fourth about equal in size and shorter than remaining segments. Fontanelle of moderate size, distinct. Labrum longer than wide, widest at basal third, tapering to the narrow, rounded, hyaline tip. Pronotum conspicuously narrower than the head, distinctly wider than long, the anterior margin with a broad median concavity, the posterior margin widely and shallowly concave. Abdomen without dark dorsal pattern.

Measurements (50 specimens).—Total length, 5·50–7·50 mm.; head, with mandibles, long, 2·75–3·30 mm.; head, without mandibles, long, 1·90–2·16 mm.; head, to fontanelle, long, 1·72–1·96 mm.; head, maximum width, 1·56–1·76 mm.; head, minimum width, 1·02–1·17 mm.; gula, minimum width, 0·26–0·42 mm.; fontanelle, wide, 0·14–0·20 mm.; pronotum, wide, 1·08–1·32 mm.; pronotum, long, 0·57–0·68 mm.

Distribution.—Western Australia, 18 miles NNW of Galena,* 25.X.1953, J. H. Calaby, workers, soldiers, and alates; 23 miles NNW of Galena, 25.X.1953, J. H. Calaby, workers and soldiers; 51 miles NNW of Galena, 25.X.1953, J. H. Calaby, workers soldiers and alates (type series); 45 miles NNW of Galena, 25.X.1953, J. H. Calaby, workers, soldiers and alates; 59 miles NNW of Galena, 24.X.1953, J. H. Calaby, workers, soldiers and reproductive nymphs; 66 miles NNW of Galena, 24.X.1953, J. H. Calaby, workers and soldiers; 67 miles NNW of Galena, 24.X.1953, J. H. Calaby, workers and soldiers.

Biology.

This species is a mound builder and, so far, is known only from a relatively small area just north of the Murchison River in the direction of Shark Bay. The mounds occur in sclerophyll woodland and mallee scrub, but not in mulga scrub, and are generally situated close to a eucalypt tree or clump of mallee. They have a thick clay outer wall, variously coloured red-brown, grey-brown, or yellow-brown, depending upon the colour of the surrounding soil, and are present on the yellowish-brown and greyish-brown soils, and less commonly on the red sandy soils, but not on the stony red soils towards the Murchison River.

The average size of the mounds is about 5 feet high and 3–4 feet diameter at ground level, whilst the largest was 8 feet high, 5 feet in diameter at ground level, and extended below ground level to a depth of 4 feet. An unusual feature is the presence of small mounds 6–9 inches in diameter and 2–6 inches high. Mounds of this small size relative to the average size have not been recorded in any of the other Australian species of *Coptotermes*.

The mound consists of two distinct regions, (i) an inner nest structure of rather loose, coarse, woody material, honeycombed with galleries but without any "nursery" area of thin-walled concentric cells, and (ii) a thick outer wall of clay. This outer wall is generally separated from the woody nest region by a distinct gap of 1–3 inches, and is traversed by only a few very large trunk galleries (up to 3 inches in diameter) that lead up towards the summit of the mound, where there is an area of small flattish galleries close to the surface. A few of these small flattish sub-surface galleries are also found here and there on the sides of the mound. Occasionally the interior of the mound gives the impression of a large cavity between the upper surface of the nest region and the outer wall. In such instances there are no trunk galleries in the outer wall itself, and this cavity is, in fact, a single very large trunk gallery communicating with the summit of the mound. Alates concentrate in the flattish galleries referred to above during the heat of the day, but appear to retreat to the central nest region at other times.

Many mounds have a zone of extremely wet clay localized within the upper portion of the outer wall. This zone, which may be a foot in diameter, is linked to the nest

* Galena is a small lead-mining town about a mile south of the Murchison River, on the north-west coastal highway.

region by the large trunk galleries, and may serve as a source of humidity or as a reserve of readily available building material to re-seal the outer wall after the release of alates.

Winged adults are present in the mounds in October.

Affinities.

The winged adult is much darker than either *C. dreghorni* Hill or *C. lacteus* (Froggatt); in addition it has one more segment in the antenna and the wing membrane is devoid of hairs. The characteristic colour and large size of the soldier head serve to distinguish it from all other Australian species of *Coptotermes*.

Types.—Holotype winged adult female and morphotype soldier and worker in the Division of Entomology Museum, C.S.I.R.O., Canberra.

AHAMITERMES INCLUSUS, sp. nov.

Winged Adult.

Not known.

Queen (Fig. 1, C).

Head and thorax golden brown, tergites of abdomen somewhat paler, sternites of abdomen, antennae and labrum light yellowish-brown. Head, thorax, and tergites and sternites of abdomen densely pubescent. Postclypeus more than half as long as wide, the anterior margin straight, the posterior margin strongly convex. Fontanelle lanceolate, with indications of anterior prolongation. Eyes moderately large and prominent. Ocelli oval, separated by about half their long diameter from the eyes. Antennae of 15 segments, third segment shortest and narrowest of all. Pronotum a little wider than the head, somewhat wider than long, the anterior margin widely and deeply concave, the sides somewhat rounded at first and then narrowed evenly to the shallowly concave posterior margin. Posterior margins of meso- and metanotum widely and deeply notched. Tibial spurs 3:2:2.

Measurements.—Head to apex of labrum, long 1·06 mm.; head, to clypeofrontal suture, long, 0·55 mm.; head, wide, 0·88 mm.; eyes, maximum diameter, 0·28 mm.; ocelli, long, 0·09 mm.; pronotum, long, 0·82 mm.; pronotum, wide, 0·93 mm.; total length, 12·50 mm.; width of abdomen, 3·75 mm.

Soldier (Fig. 1, D).

Head light orange, mid-dorsal area paler, the entire head capsule occasionally lightly suffused with brown. Basal third of mandibles light orange, distal two-thirds pale ferruginous. Head almost parallel-sided or with sides very slightly concave. Fontanelle distinct. Labrum a little wider than long, bluntly conical, the hyaline tip usually with an obvious concavity. Mandibles relatively short and stout, about two-thirds as long as the head capsule, generally with vestiges of teeth about the middle. Post-clypeus strongly bilobed. Antennae short, extending for only about one-fifth of their length beyond the tips of the mandibles, of 13 segments, third segment smallest of all. Pronotum about twice as wide as long, a little narrower than the head, the anterior margin convex, the posterior margin shallowly concave. Tibial spurs 3:2:2.

Measurements (30 specimens).—Total length, 4·00–5·00 mm.; head, with mandibles, long, 1·70–1·83 mm.; head, to clypeofrontal suture, long, 1·02–1·10 mm.; head, wide, 0·66–0·77 mm.; pronotum, long, 0·31–0·35 mm.; pronotum, wide, 0·60–0·69 mm.

Distribution.—Western Australia, 51 miles NNW of Galena, 25.X.1953, J. H. Calaby, workers, soldiers, reproductive nymphs, and queen (type series); 66 miles NNW of Galena, 24.X.1953, J. H. Calaby, workers and soldiers.

Biology.

This species is known from two series only, both of which were taken from termitaria of *Coptotermes brunneus*, sp. nov. One series was collected from a concentration of cells in the outer clay wall of the *Coptotermes* mound, the other from a definite nest structure about a foot in diameter situated on top of the cellular portion of a *Coptotermes* nest. This second series consisted of a queen, reproductive nymphs,